

AN EXAMPLE OF CLINAL VARIATION IN EASTERN NORTH AMERICAN BUCKMOTHS (SATURNIIDAE: *HEMILEUCA*)

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ABSTRACT. Morphological variation in populations of eastern North American buckmoths was examined. Samples of 25 males each were analyzed from four points along a north-south line approximately 800 km long from Schoolcraft Co., Michigan to Vinton Co., Ohio. Clinal variation was demonstrated from higher to lower latitudes: (1) forewing length from smaller to larger; (2) forewing white band width from wider to narrower; and (3) darkness of the black background of the wing from lighter to darker. No logical way was found to separate these four populations into subspecies or species based on morphological characters.

Additional key words: *Hemileuca maia*, *H. nevadensis*, *H. lucina*.

The black and white buckmoths of the eastern United States and Canada have attracted much attention because of their showy wing patterns and unusual flight period very late in the season. Three species are usually attributed to eastern North America: in the western part *Hemileuca nevadensis* Stretch, in the northeast *H. lucina* Hy. Edw., and in the remainder of the area *H. maia* (Drury) (Ferguson 1971, Covell 1984). Each species is generally associated with a distinct food plant, all unrelated: willows (*Salix*: Salicaceae), meadowsweets (*Spiraea*: Rosaceae), and oaks (*Quercus*: Fagaceae), respectively.

We have surveyed various habitats and have verified, by egg mass placement and larval feeding, a more diverse range of food plants than is usually assumed (Scholtens & Wagner 1994). In addition, several populations are difficult to assign to any of the three recognized North American species. Some appear to be intermediate in maculation between *H. nevadensis* and *H. lucina* and others between *H. nevadensis* and *H. maia*. Here, using data on the characters typically used to distinguish the presently recognized species, we test the hypothesis that the populations in the Great Lakes region consist of a single species forming a cline ranging from relatively small, 'washed-out' looking forms in the north to larger, heavily marked forms in the south.

MATERIALS AND METHODS

We sampled and studied buckmoths at four localities in the Great Lakes region. From north to south these were: (1) Schoolcraft County in the Upper Peninsula of Michigan; (2) Roscommon County in the



FIG. 1. Map of sampling localities and example of male buckmoth from each.

central Lower Peninsula; (3) Washtenaw County in the southern Lower Peninsula; and (4) Vinton County in southern Ohio (Fig. 1). At each locality we made notes on the habitat and host plants used by the buckmoths and collected a series of 40–50 males, from which a sample of 25 in good condition were chosen for measurements and visual assessment. Vouchers from each population have been deposited at the University of Michigan Museum of Zoology.

A video image of each specimen was stored on a Macintosh II computer using the program NEH Image version 1.26. The lighting arrangement and the specimen-camera distance were not changed during image capture. For each image, measurements were taken, using Image, of forewing length from the base of the wing to the farthest point on the wing tip, and width of the white band on the forewing and hindwing along veins M_1 and CU_2 . The limits of the white band were easily determined by a sharp change over in scale color, even in the most diffusely

patterned moths. In addition, 10 pixel by 10 pixel areas were marked off on the forewing between veins CU_1 and CU_2 inside the white band and immediately distal to the white band. Using Image, an average darkness for each 100 pixel area was calculated based on a 256 point gray scale.

Because one characteristic difference between the populations was wing darkness, we did a microscopic examination of scale sizes and densities for the three Michigan populations, covering most of the variation in darkness. For 10 specimens from each population, we counted all scales in a 1.42×2.16 mm area of the forewing between veins M_3 and CU_1 , centered on the white band. In addition for 5 specimens from each population, 10 scales in one field of view were measured for length and width. For all data, comparisons among localities were made by ANOVA using the statistical package SYSTAT 5.0 for the Macintosh.

RESULTS

A great deal of variation exists in the habitats and host plants of Great Lakes buckmoths compared to previously published data. In the northern part of the range through southern Michigan, habitats are mainly wetlands, similar to those typically used by the western *H. nevadensis*, while in the south, upland wooded areas are prevalent. The host plants in wetland areas include willow, poplar, meadowsweet, and bog birch, and in the dry wooded sites, oaks (Scholtens & Wagner 1994).

Forewing length in the sampled populations varied from a mean of 24.04 mm in northern Schoolcraft County to 26.59 mm in southern Vinton County (Fig. 2). ANOVA shows that forewing length increases significantly from north to south ($F = 20.30$, $P = <0.001$). The width of the white band on the forewing decreases significantly from north to south (on M_1 : $F = 40.96$, $P = <0.001$; on CU_2 : $F = 24.47$, $P = <0.001$). On vein M_1 the mean width is 2.17 mm in Schoolcraft County and 0.61 mm in Vinton County. On vein CU_2 the mean width is 4.42 mm in Schoolcraft County and 2.60 mm in Vinton County (Fig. 3). Although the width of the white band on the hindwing varies significantly among the three populations (on M_1 : $F = 2.79$, $P = 0.045$; on CU_2 : $F = 15.30$, $P = <0.001$), we saw no demonstrable trend from north to south (Fig. 4).

There is a significant increase in the darkness of the white band from north to south ($F = 5.04$, $P = 0.003$), varying from Schoolcraft County with a mean of 82.97 gray scale units (out of 256) to Vinton County at 88.19 units. There is a much more pronounced significant increase in the darkness of the black areas of the wing from north to south ($F = 142.28$, $P < 0.001$), varying from 112.34 units in Schoolcraft County to 164.12 units in Vinton County (Fig. 5), with most of the change occurring from northern to southern Michigan. These means hide a great

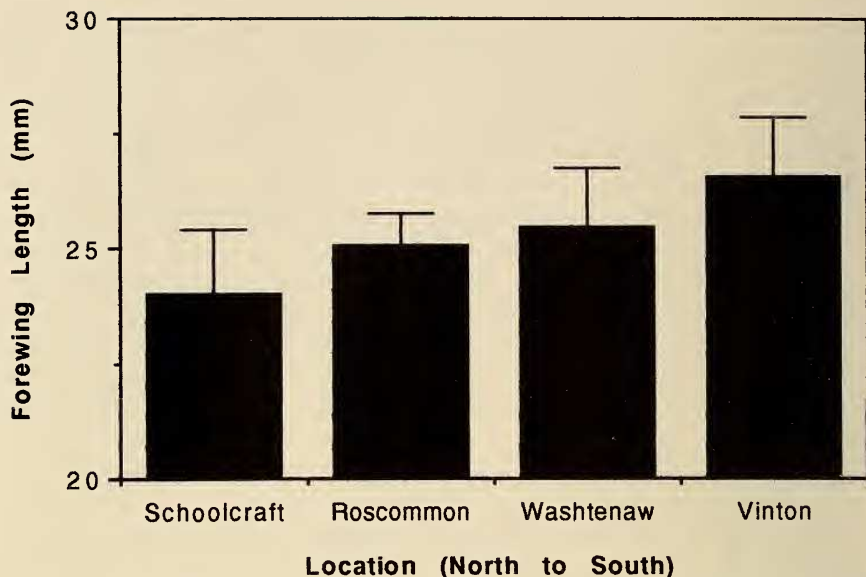


FIG. 2. Mean forewing length of sampled populations (error bars indicate standard deviation).

deal of variation in the darkness of the black areas of the wing, enough so that wing darkness overlaps in all adjacent populations (Fig. 6).

Darker wing color in the southern buckmoth populations is due to the size and distribution of wing scales. There are substantial differ-

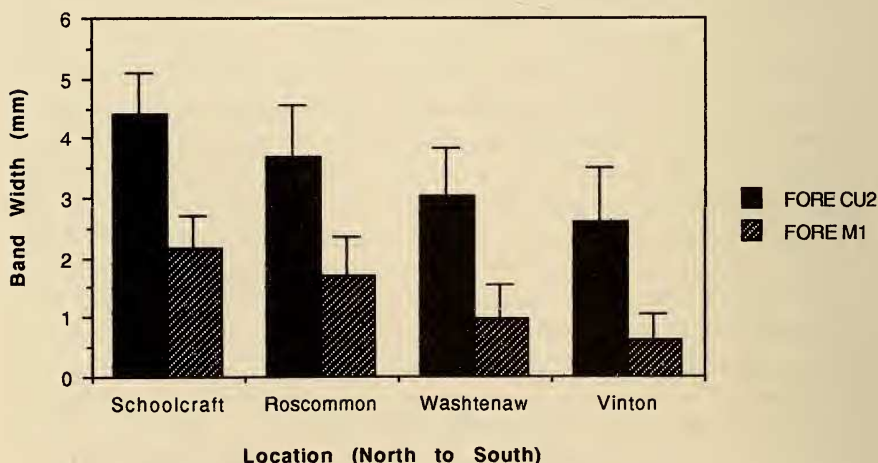


FIG. 3. Mean width of white band on forewing veins CU₂ and M₁ (error bars indicate standard deviation).

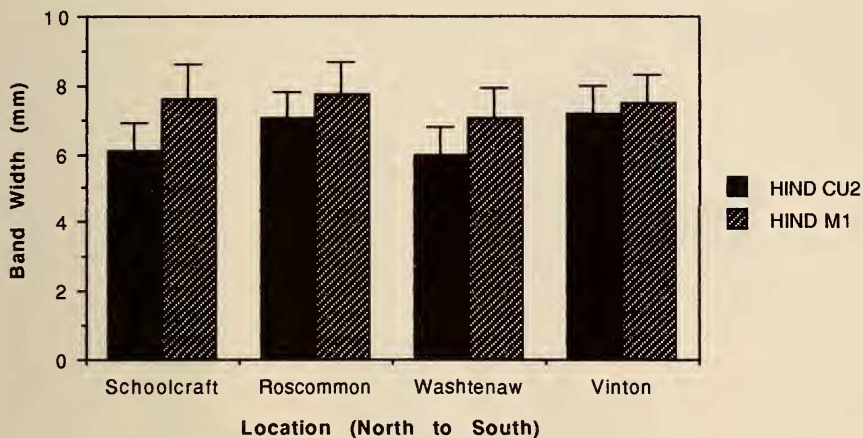


FIG. 4. Mean width of white band on hindwing veins CU_2 and M_1 (error bars indicate standard deviation).

ences in both size and density of scales among the populations (Figs. 7 and 8). From north to south, scale length ($F = 23.97$, $P = <0.001$), width ($F = 7.30$, $P = 0.008$) and density ($F = 26.97$, $P = <0.001$) increase significantly. All three of these parameters contribute to the lighter, more translucent appearance of the wings in the north.

Increasing forewing band width with decreasing wing length accentuates the trend of lighter colored wings in the north, and in Vinton County the ratio of band width to wing length is half or less of that in

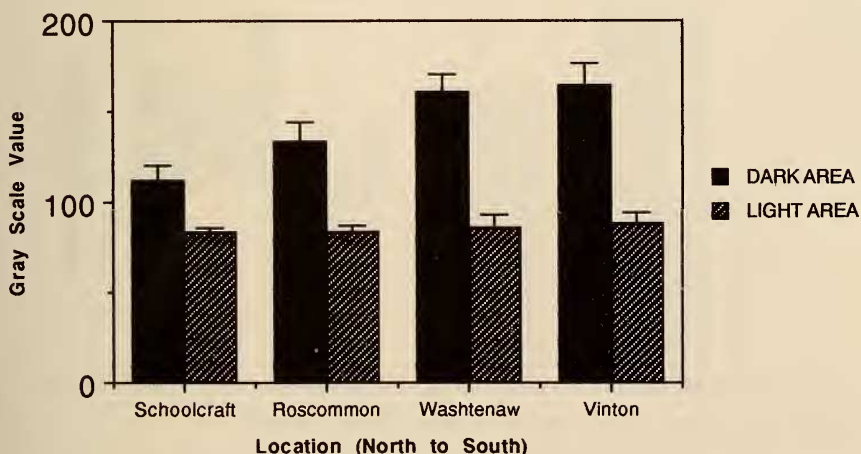


FIG. 5. Mean darkness of light and dark areas of forewing (error bars indicate standard deviation).

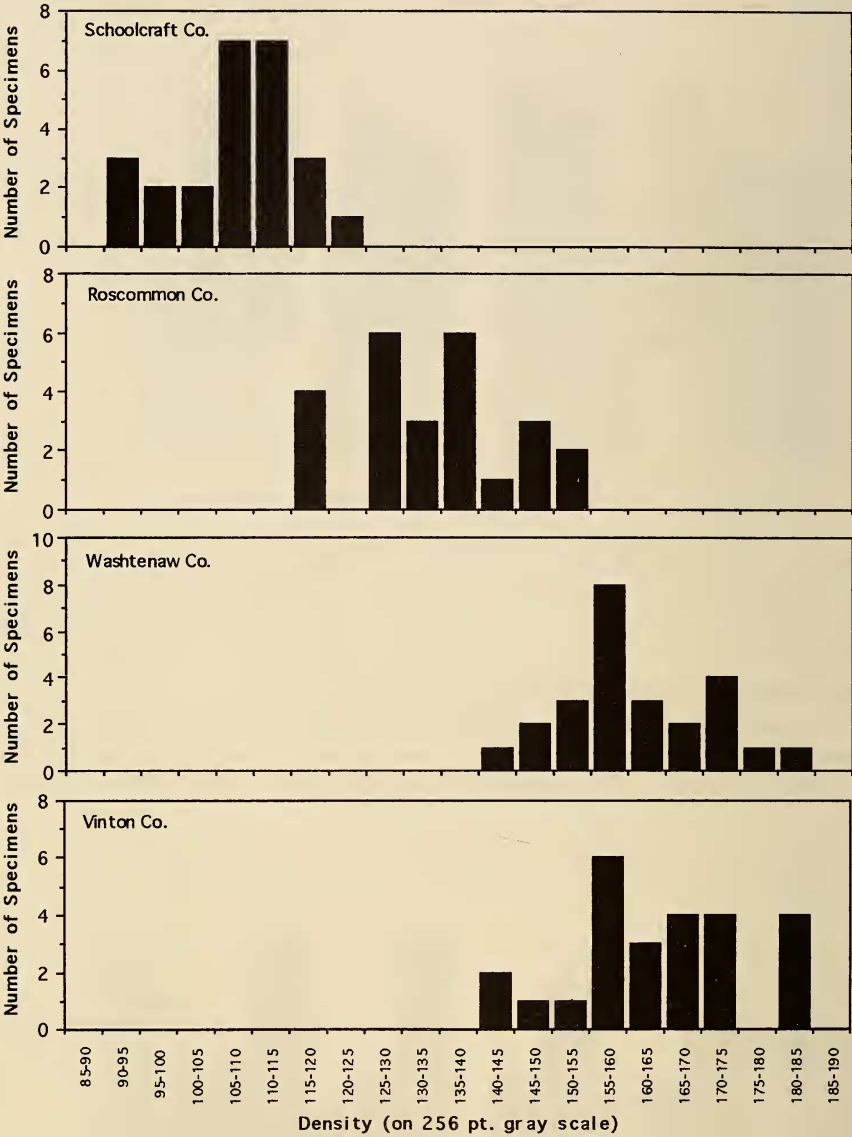


FIG. 6. Distribution of wing darkness at the four study sites.

Schoolcraft County. Also influencing this impression is a proportionally greater increase in width at the center of the white band as you proceed north. The ratio of the width of the white band on vein M_1 to the width on vein CU_2 decreases to less than half of the Schoolcraft County value in Vinton County.

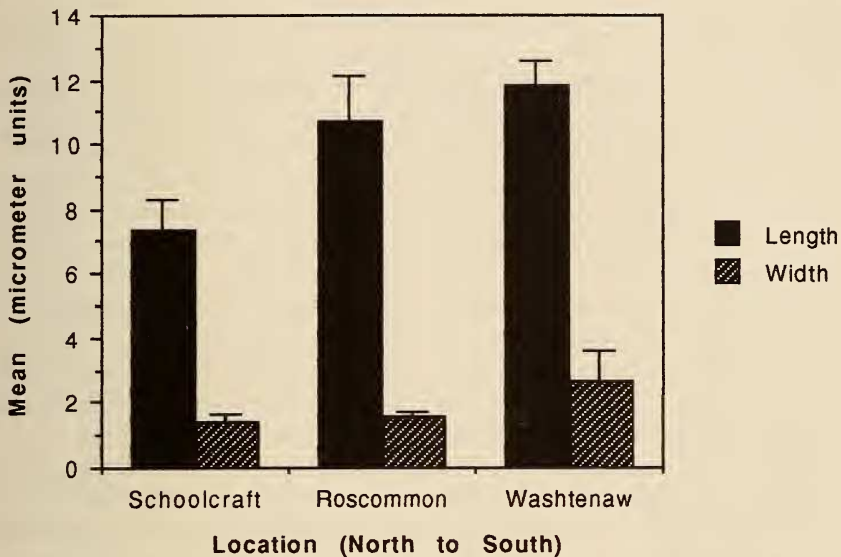


FIG. 7. Mean scale length and width (error bars indicate standard deviation).

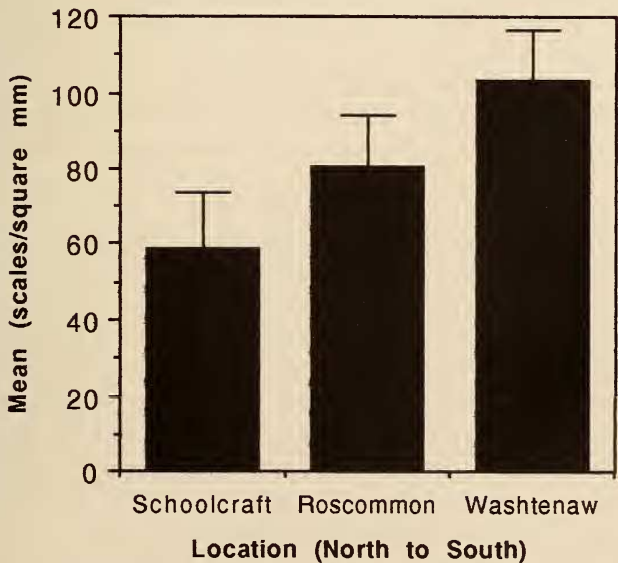


FIG. 8. Mean scale density (error bars indicate standard deviation).

DISCUSSION

Our results clearly demonstrate correlated changes in food plants and maculation characters of buckmoths along a north-south line in the Great Lakes region. Where the wing length is smaller in the north, the white band is wider and the black background is paler. The northernmost element is most similar to the New England buckmoth, *Hemileuca lucina*, the southernmost element is most similar to *H. maia*, and the intermediates resemble some of the forms of the widespread western buckmoth, *H. nevadensis*. There is also a general correlation with habitat, bogs and fens in the north and upland, oak woods in the south. The larval food plants include bog birch (*Betula pumila* L.: Betulaceae), willows (*Salix* spp.) and meadowsweets (*Spiraea* spp.) northward and oaks (*Quercus* spp.) in the south (Scholtens & Wagner 1994).

Change in maculation of buckmoths is a direct result of a change in scale size and density. Scale density in the northern populations decreases, even when corrected for the reduction in wing size, and scale size also decreases proportionally much more than wing size. The existence of a north-south morphological cline in *Hemileuca* should not be surprising. Good examples of latitudinal clines exist in other widespread species in North America (e.g., *Cercyonis*, Emmel 1969), Great Britain (e.g., *Coenonympha*, Porter 1980), and Australia (e.g., *Tisiphone*, Lucas 1969). In our experience, forms of non-migratory species in the extreme north tend, in general, to be smaller and the pattern less contrasting than those from the south. The same is often true of spring versus summer forms.

Some speculations about possible evolutionary causes of size and maculation changes in northern populations are the following: (1) smaller size may simply be a result of a shorter growing season; and (2) scale development may be aborted because of the shorter pupal period in northern populations (late June through late August in the north versus mid-June through early October in the south). These remain speculations until experimental work can verify or refute them.

Confusion about the nomenclature of *Hemileuca* populations has existed for many years as evidenced by the naming of *H. latifascia* Barnes and McDunnough as a subspecies of *H. lucina*, followed by its synonymization with *H. nevadensis* (Ferguson 1971). Forbes (1960) even remarked on the intermediacy of *H. latifascia* between *H. maia* and *H. lucina*. Great Lakes populations have always been vexing because willow feeders have periodically been reported from the region (Ely 1954, Riley 1873, Worthington 1878), but not studied carefully. Our data show that no good maculation differences exist that allow Great Lakes populations to be placed confidently into one of the recognized species. Likewise, the host

plants and habitats are not distinctive and do not serve to identify populations definitively as once thought. Ferge (1981) documented similar within population variation in Wisconsin, and populations in Minnesota, and the eastern United States also resemble those we studied. Legge et al. (1996), in a study examining allozyme differences in *Hemileuca* populations from across the country, found very few differences between any of the populations examined, and suggested that these populations could still be considered distinct species based on ecological differences. Our data would not support this, showing that ecological differences among the various populations are not consistent (Scholtens & Wagner 1994). Although separate eastern populations may seem quite distinct, local population differentiation may be more prevalent in this region because of longer isolation due to habitat fragmentation.

The patterns seen in this study could result from variation within a single species or from a hybrid zone between distinct species. Our data cannot distinguish between these alternatives, but the most satisfying explanation for our findings is that all populations represent a single species showing clinal variation from north to south. A species distinction could exist between the wetland populations that feed on birch, poplar, meadowsweet and willow and the upland, oak-feeding populations. Ecologically, these appear distinct and some evidence indicates that they may be isolated by pheromone differences (James Tuttle, pers. comm.), but these differences are not indicated by the clinal nature of the morphological variation. If all populations are a single species they would be referred to as *H. maia* (Drury). If two entities exist, the upland populations would be *H. maia* (Drury) and the wetland ones *H. nevadensis* Stretch. This question may be decided conclusively by careful hybridization and rearing studies between geographically close populations of both types.

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